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UNITED STATES DEPARTMENT OF AGRICULTURE

SUPPRESSION OF PEST POPULATION WITH STERILE MALE INSECTS

By WALDEMAR KLASSEN and JAMES F. CREECH [1]

In order to plan large-scale field experiments to evaluate the use of sterile male insects for suppression of a pest population, one must know the level of male sterility and the magnitude of the release ratio required to eradicate the target population. The magnitude of these variables depends on the rate of increase of the pest population. The rate of increase is determined by the number of eggs laid by the female and by the action of weather, predators, parasite diseases, and other mortality factors. Obviously the rate of increase is subject to wide fluctuation between localities, between consecutive generations, and between years. We must know what is required in terms of the release ratios and the levels of sterility to deal with populations undergoing average or explosive rates of increase. (The rate of increase is defined as one-half the number of progeny produced by a female.)

PROCEDURES

To fulfill this need, we have computed a number of cases in which we assume that we are dealing with a target area of 1,000 acres on which the pest population has been reduced to 1,000 males and 1,000 females. This population may have from one to five generations per year. The release ratios at the outset of the program are 100:1, 50:1, 25:1, and 12.5:1 (sterile males:native males; females if released are fully sterile). The level of male sterility is 90, 95, 98, 99, and 100 percent, and the rate of increase from generation to generation is fivefold, tenfold, twentyfold, and fortyfold. This type of model was employed by Knipling.[2] Other models were presented by Berryman [3] and Lawson.[4]

In some instances we may be able to constitute a release strain with a dominant conditional lethal trait. Such a lethal trait would provide an additional mortality factor that could insure the success of the eradication program when sterility alone would be inadequate to completely suppress the population. We have shown in considerable detail how such conditional lethal traits under monofactorial or polygenic control could be used if partially sterile males and females were released.[5] [6]

[1] Waldemar Klassen, entomologist, Entomology Research Division, Agricultural Research Service, and James F. Creech, graduate student, Department of Electrical Engineering, North Dakota State University.

The use of a digital computer was made possible through the cooperative agreement between North Dakota State University, Fargo, and the Metabolism and Radiation Research Laboratory, Agricultural Research Service.

[2] KNIPLING, E. F. SOME BASIC PRINCIPLES IN INSECT POPULATION SUPPRESSION. Ent. Soc. Amer. Bul. 12: 7–15. 1966.

[3] BERRYMAN, A. A. MATHEMATICAL DESCRIPTION OF THE STERILE-MALE PRINCIPLE. Canad. Ent. 99: 858–865. 1967.

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[5] KLASSEN, W., CREECH, J. F., and BELL, R. A. THE POTENTIAL FOR GENETIC SUPPRESSION OF INSECT POPULATIONS BY THEIR ADAPTATIONS TO CLIMATE. U.S. Dept. Agr. Misc. Pub. 1178, 77 pp. 1970.

[6] KLASSEN, W., KNIPLING, E. F., and MCGUIRE, J. U. THE POTENTIAL FOR INSECT POPULATION SUPPRESSION BY DOMINANT CONDITIONAL LETHAL TRAITS. Ent. Soc. Amer. Ann. 63: 238–255. 1970.

In this study we consider the effect of releasing only partially sterile males with a conditional lethal trait determined by a single dominant gene. In all other respects the model used is identical to that of Klassen et al.[7] We assume that the release strain may not be completely homozygous for this gene and that the frequency (q) of the native type allele in the release strain is 0.223606, 0.100000, or 0.031622. According to the Hardy-Weinberg equilibrium, the respective frequencies (q^2) of the native genotypes (dd) in such strains would be 5, 1, or 0.1 percent. For our example, we assume that all Dd and DD insects cannot enter diapause and that they perish during the winter. We also assume that five releases are made to coincide with the overwintered parental, F_1, F_2, F_3, and F_4 generations. All computations were made by means of a digital computer, using the methods of Klassen et al.[7]

RESULTS AND DISCUSSION

Table 1 shows that when the population increases fivefold per generation, a downward trend in numbers can be induced in all cases calculated, including case 16 with releases of 12,500 90-percent sterile males per generation. After just one release of 100,000 completely sterile males, theoretical extinction is achieved. Two releases of 50,000 or 25,000 completely sterile males are required to achieve theoretical extinction, and three releases of 12,500 completely sterile males achieve this result. In actual practice the population would be completely suppressed when the density was too low to permit individuals of the opposite sex from meeting. The magnitude of this density would depend on the species and other factors. Complete suppression in a single season may be achieved with lower release ratios and lower levels of sterility in multivoltine populations than in monovoltine or bivoltine populations.

When the population increases tenfold per generation, a downward trend cannot be induced if the released males are only 90-percent sterile. However, with 98-percent sterility, a downward trend can be induced with only 12,500 sterile males per release. When 12,500 completely sterile males are released per generation, four or five releases are required to achieve extinction compared with three releases of 25,000 completely sterile males, two releases of 50,000 completely sterile males, and one or two releases of 100,000 completely sterile males.

When the population increases twentyfold per generation, downward trends can be induced by releasing 100,000 or 50,000 98-, 99-, or 100-percent sterile males or by releasing 25,000 99- or 100-percent sterile males. When 100,000 or 50,000 males are released, complete suppression would require two or three more releases of 99-percent sterile males than of 100-percent sterile males.

When the population increases fortyfold per generation, a downward trend would be induced in just three cases: Releases of 100,000 99- or 100-percent sterile males and 50,000 100-percent sterile males. With this very high rate of increase, complete sterility would probably be required to achieve complete suppression. Thus table 1 clearly illustrates the need to adjust the release ratio to the rate of increase and to the level of sterility attainable without serious damage to the males.

There may be instances when the induction of a high level of sterility impairs the competitiveness of males. In order to suppress populations in such instances, we must decide whether the high level of sterility is mandatory. If such is required, we would compensate for impaired competitiveness by increasing the release ratio. By considering cases in table 1 in which the population increases tenfold per generation, we can estimate the effect of impaired competitiveness. The release of 100,000 50-percent competitive insects is equivalent to the release of 50,000 fully competitive insects. Similarly 100,000 25-percent competitive insects are equivalent to 25,000 fully competitive insects and 100,000 12.5-percent competitive insects are equivalent to 12,500 fully competitive insects.

Table 1 shows that when the rate of increase is tenfold, the release of 100,000 95-percent

[7] See footnote 5.

TABLE 1.—*Population trends when native population of 1,000 males and 1,000 females is overflooded in each generation by 100,000, 50,000, 25,000, or 12,500 partially or completely sterile males*

Case No.	Males released	Sterility	Rate of increase	Progeny in each generation				
				F_1	F_2	F_3	F_4	F_5
	Number	*Percent*		*Number*	*Number*	*Number*	*Number*	*Number*
1	100,000	90	Fivefold	1,089	571	293	148	75
2	100,000	95	do	594	157	40	10	2
3	100,000	98	do	297	32	3	0	0
4	100,000	99	do	198	11	1	0	0
5	100,000	100	do	99	0	0	0	0
6	50,000	90	do	1,176	650	344	177	90
7	50,000	95	do	686	194	50	13	3
8	50,000	98	do	392	47	5	0	0
9	50,000	99	do	294	19	1	0	0
10	50,000	100	do	196	2	0	0	0
11	25,000	90	do	1,346	832	477	259	135
12	25,000	95	do	865	286	79	20	5
13	25,000	98	do	577	90	10	1	0
14	25,000	99	do	481	47	3	0	0
15	25,000	100	do	385	15	0	0	0
16	12,500	90	do	1,667	1,302	941	624	381
17	12,500	95	do	1,204	564	200	58	15
18	12,500	98	do	926	255	38	4	0
19	12,500	99	do	833	174	15	1	0
20	12,500	100	do	741	107	2	0	0
21	100,000	90	Tenfold	2,178	2,389	2,643	2,954	3,340
22	100,000	95	do	1,188	661	351	181	92
23	100,000	98	do	594	136	28	6	1
24	100,000	99	do	396	47	5	0	0
25	100,000	100	do	198	2	0	0	0
26	50,000	90	do	2,353	2,840	3,545	4,638	6,488
27	50,000	95	do	1,373	863	502	275	144
28	50,000	98	do	784	217	48	10	2
29	50,000	99	do	588	93	10	1	0
30	50,000	100	do	392	15	0	0	0
31	25,000	90	do	2,692	3,930	6,508	13,255	38,252
32	25,000	95	do	1,731	1,415	1,078	755	484
33	25,000	98	do	1,154	486	143	33	7
34	25,000	99	do	962	276	43	5	0
35	25,000	100	do	769	117	3	0	0
36	12,500	90	do	3,333	6,863	20,166	101,200	831,571
37	12,500	95	do	2,407	3,213	5,082	10,696	35,794
38	12,500	98	do	1,852	1,622	1,293	882	471
39	12,500	99	do	1,667	1,198	662	235	45
40	12,500	100	do	1,481	829	266	28	0
41	100,000	90	Twentyfold	4,356	10,385	29,995	130,406	1,187,253
42	100,000	95	do	2,376	2,906	3,697	4,972	7,264
43	100,000	98	do	1,188	613	282	120	50
44	100,000	99	do	792	220	49	10	2
45	100,000	100	do	396	16	0	0	0
46	50,000	90	do	4,706	13,219	54,218	451,536	7,557,089
47	50,000	95	do	2,745	4,139	7,264	16,609	61,558

TABLE 1.—*Population trends when native population of 1,000 males and 1,000 females is overflooded in each generation by 100,000, 50,000, 25,000, or 12,500 partially or completely sterile males*—Continued

Case No.	Males released	Sterility	Rate of increase	Progeny in each generation				
				F_1	F_2	F_3	F_4	F_5
	Number	*Percent*		*Number*	*Number*	*Number*	*Number*	*Number*
48	50,000	98	do	1,569	1,102	676	360	169
49	50,000	99	do	1,176	506	152	35	7
50	50,000	100	do	784	122	3	0	0
51	25,000	90	do	5,385	20,192	144,942	2,229,679	43,713,314
52	25,000	95	do	3,462	7,720	27,338	210,949	3,451,016
53	25,000	98	do	2,308	2,919	4,322	8,470	27,435
54	25,000	99	do	1,923	1,795	1,591	1,289	899
55	25,000	100	do	1,538	918	331	44	1
56	12,500	90	do	6,667	38,596	498,826	9,548,004	190,511,260
57	12,500	95	do	4,815	19,588	183,090	3,243,874	64,406,113
58	12,500	98	do	3,704	10,848	68,683	1,014,428	19,810,336
59	12,500	99	do	3,333	8,431	43,789	560,673	10,739,599
60	12,500	100	do	2,963	6,279	25,210	253,155	4,608,045
61	100,000	90	Fortyfold	8,713	47,946	525,549	15,806,680	625,157,160
62	100,000	95	do	4,752	13,697	60,753	659,386	20,544,136
63	100,000	98	do	2,376	2,995	4,128	6,574	13,460
64	100,000	99	do	1,584	1,127	701	377	179
65	100,000	100	do	792	125	3	0	0
66	50,000	90	do	9,412	66,793	1,230,089	45,874,200	1,831,375,800
67	50,000	95	do	5,490	21,838	192,420	5,196,311	204,124,180
68	50,000	98	do	3,137	6,251	19,415	139,272	3,289,192
69	50,000	99	do	2,353	3,083	4,885	10,964	47,283
70	50,000	100	do	1,569	969	372	55	1
71	25,000	90	do	10,769	111,782	3,227,580	127,330,660	5,091,427,200
72	25,000	95	do	6,923	45,842	924,895	35,193,230	1,405,831,900
73	25,000	98	do	4,615	18,982	219,932	7,200,348	286,067,430
74	25,000	99	do	3,846	12,418	102,795	2,779,722	109,243,840
75	25,000	100	do	3,077	7,135	35,640	593,270	21,886,250
76	12,500	90	do	13,333	220,290	8,003,322	319,235,700	12,768,528,000
77	12,500	95	do	9,630	121,014	4,053,218	161,184,550	6,446,432,000
78	12,500	98	do	7,407	72,296	2,163,660	85,577,594	3,422,124,000
79	12,500	99	do	667	58,246	1,637,138	64,510,391	2,579,426,000
80	12,500	100	do	5,926	45,420	1,171,822	45,893,778	1,834,751,700

sterile, fully competitive insects to each generation would yield 92 F_5 progeny. Similarly with a tenfold rate of increase, the release of 100,000 98-percent sterile insects to each generation with 100-, 50-, 25-, or 12.5-percent competitiveness would yield 1, 2, 7, or 471 F_5 progeny, respectively. Thus 98-percent sterile males with 25-percent competitiveness would probably cause complete population suppression, whereas 95-percent sterility with full competitiveness might not. However, if the rate of increase between generations is only fivefold, the release of 100,000 95-percent sterile, fully competitive males would yield two F_5 progeny. In this case the high level of sterility would not be required.

Table 2 illustrates the bonus effect of employing a release strain with a dominant conditional lethal trait. In cases 2, 3, 12, and 20, substantial suppression of a population with four or five generations per year is achieved,

TABLE 2.—*Population and genotypic trends when native population of 1,000 males and 1,000 females is overflooded in each generation by partially sterile males bearing dominant allele for inability to diapause*

Case No.	Males released	Sterility	Rate of increase	q^{2} [1]	Progeny in each generation with indicated genotype														
					F_1			F_2			F_3			F_4			F_5		
					dd	*Dd*	*DD*	*dd*	*Dd*	*DD*	*dd*	*Dd*	*DD*	*dd*	*Dd*	*DD*	*dd*	*Dd*	*DD*
	Number	*Percent*			*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
1	100,000	90	Tenfold	0.05	641	1,537	0	410	1,360	620	300	1,263	1,080	248	1,249	1,457	230	1,305	1,806
2	100,000	90	do	.01	396	1,782	0	209	1,348	833	126	1,066	1,452	86	910	1,957	68	847	2,426
3	100,000	90	do	.001	261	1,918	0	112	1,314	964	53	909	1,681	29	659	2,266	17	514	2,809
4	100,000	90	Twentyfold	.05	1,282	3,075	0	2,012	5,805	2,568	4,385	14,691	10,920	16,527	60,205	53,673	144,239	539,435	503,579
5	100,000	90	do	.01	792	3,564	0	1,152	5,782	3,450	2,323	12,999	14,673	8,303	49,979	72,124	71,122	439,443	676,689
6	100,000	90	do	.001	521	3,835	0	733	5,657	3,995	1,420	11,588	16,988	4,922	41,984	83,500	41,641	362,195	783,417
7	100,000	95	Tenfold	.05	419	769	0	121	384	156	40	171	140	15	77	90	6	36	51
8	100,000	95	do	.01	297	891	0	64	387	209	16	146	189	5	55	121	2	23	68
9	100,000	95	do	.001	229	959	0	36	382	242	6	126	219	1	40	140	0	13	79
10	100,000	95	Twentyfold	.05	839	1,537	0	611	1,648	648	519	1,838	1,340	519	2,230	2,223	617	3,031	3,617
11	100,000	95	do	.01	594	1,782	0	365	1,671	871	260	1,636	1,801	220	1,765	2,988	226	2,178	4,860
12	100,000	95	do	.001	459	1,918	0	243	1,655	1,008	146	1,466	2,085	103	1,410	3,459	89	1,549	5,626
13	100,000	98	do	.05	573	615	0	155	353	104	41	146	95	11	54	55	4	20	26
14	100,000	98	do	.01	475	713	0	102	371	140	20	135	127	4	42	74	1	13	35
15	100,000	98	do	.001	421	767	0	74	376	162	10	124	148	1	34	85	0	9	41
16	100,000	98	Fortyfold	.001	842	1,534	0	552	1,739	704	434	2,006	1,688	440	2,672	3,462	654	4,750	8,056
17	100,000	98	do	.01	950	1,426	0	678	1,709	608	584	2,086	1,458	646	2,938	2,990	1,030	5,472	6,959
18	100,000	99	do	.001	817	767	0	301	649	177	86	372	243	18	157	202	3	52	124
19	50,000	90	Tenfold	.01	588	1,765	0	355	1,633	852	247	1,567	1,731	202	1,640	2,796	198	1,931	4,360
20	50,000	90	do	.001	454	1,899	0	236	1,618	986	138	1,404	2,004	94	1,307	3,237	76	1,365	5,047
21	50,000	95	Twentyfold	.001	846	1,899	0	683	2,385	1,070	733	3,443	3,088	1,195	6,759	8,655	3,714	23,011	34,833
22	50,000	98	do	.05	960	609	0	426	565	111	162	363	152	54	181	125	17	76	76
23	50,000	98	do	.01	863	706	0	339	614	150	108	365	204	28	164	168	7	60	102
24	50,000	98	do	.001	809	760	0	293	636	173	82	359	236	17	149	194	3	48	118
25	50,000	98	Fortyfold	.001	1,618	1,519	0	2,251	3,205	794	5,683	9,822	3,911	37,816	69,666	31,790	883,098	1,642,504	763,590
26	50,000	99	do	.001	1,593	760	0	1,546	1,337	200	1,930	2,336	619	3,698	5,388	1,878	14,800	23,352	9,131
27	25,000	90	Fivefold	.05	600	747	0	198	479	155	67	244	166	24	115	119	10	54	71
28	25,000	90	Tenfold	.001	830	1,862	0	641	2,269	1,020	637	3,076	2,795	898	5,321	7,036	2,091	13,876	22,285
29	25,000	95	do	.05	984	747	0	503	746	167	244	573	260	113	375	266	51	219	214
30	25,000	95	do	.01	865	865	0	388	803	224	160	568	350	60	337	358	22	175	288

31	25,000	95	do	.001	800	931	0	329	827	260	119	554	405	37	304	415	10	141	333
32	25,000	98	do	.05	855	299	0	241	218	27	40	79	25	5	17	11	1	3	3
33	25,000	98	Twentyfold	.001	1,563	745	0	1,455	1,272	191	1,678	2,083	561	2,755	4,198	1,517	8,111	13,654	5,670
34	25,000	99	do	.05	1,624	299	0	1,288	476	31	965	557	68	654	537	99	372	419	108
35	25,000	99	do	.01	1,577	346	0	1,213	540	42	878	621	92	571	586	133	308	446	145
36	25,000	99	do	.001	1,551	372	0	1,173	574	48	832	653	106	527	608	154	274	457	168
37	12,500	90	Fivefold	.05	948	719	0	457	690	155	208	502	232	90	309	226	38	170	172
38	12,500	90	do	.01	833	833	0	352	742	208	134	496	312	46	275	303	16	134	231
39	12,500	90	do	.001	770	897	0	296	765	241	98	483	361	27	246	351	7	106	268
40	12,500	98	Tenfold	.05	1,564	288	0	1,158	436	28	769	466	59	424	382	75	173	230	67
41	12,500	98	do	.01	1,519	333	0	1,089	495	38	696	518	79	365	415	101	138	242	91
42	12,500	98	do	.001	1,493	359	0	1,052	526	44	657	544	91	334	430	117	120	246	105

[1]Frequency of *dd* genotypes in release strain.

even though the population gradually increases throughout the season. In these cases the release ratio is high, the frequency of the conditional lethal allele in the release strain is very high, and the native population increases tenfold per generation in three of these cases and twentyfold in the other. On the other hand, complete suppression is assured when the release strain is far from homozygous for the conditional lethal allele ($q^2 = 0.05$) in cases 22, 27, and 37.

Cases 1, 2, and 3 in table 2 illustrate the desirability of using a release strain that approaches homozygozity for the conditional lethal allele. In these cases if the population has four or five generations per year, complete suppression would not be achieved if q^2 is 0.05. Complete suppression might be achieved when q^2 is 0.01, and complete suppression would almost certainly be achieved if q^2 is 0.001.

If we assume that a population of fewer than 100 individuals in the fall generation will be eradicated because of mortality during the winter and that a population of more than 100 will survive, then the presence of the dominant conditional lethal allele will assure complete suppression in a population with four or five generations per year in cases 3, 18, 22, 23, 24, 27, 29, 30, 31, 37, 38, and 39. Complete suppression would have been achieved without the conditional lethal allele in cases 7, 8, 9, 13, 14, 15, and 32. Cases in which the use of a dominant conditional lethal allele would be useful in suppressing populations that have only two or three generations per year may be ascertained by inspecting table 2. If the population has only two generations per year, complete suppression cannot be achieved in a single season without very high release ratios, a high level of sterility, and a high frequency of the conditional lethal allele.

SUMMARY

To evaluate the use of sterile male insects for suppression of a pest population, one must know the magnitude of the release ratio and the level of male sterility required to eradicate the target population. The magnitude of these variables depends on the rate of increase of the pest population. The interrelationships between the release ratio, the level of sterility, and the rate of increase are quantitatively illustrated.

Generally if low release ratios must be used to suppress a pest population, a higher level of sterility is required than when high release ratios may be used. On the other hand, if high release ratios may be used, the level of sterility required for population suppression may be lower than if low release ratios must be used. When the rate of increase of the pest population is high, it is frequently more advantageous to impair competitiveness in order to achieve a high level of sterility than to use a slightly lower level of sterility with full competitiveness. A considerable bonus effect would be realized by constituting a release strain with a dominant conditional lethal trait.

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